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PROPAGATION AND REINTRODUCTION OF THE ENDANGERED HEMIPARASITE *SCHWALBEA AMERICANA* (SCROPHULARIACEAE)

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ABSTRACT. Propagation of the endangered hemiparasite *Schwalbea americana* was conducted in the presence of several species of potential host plants. Seeds were germinated and the seedlings transferred to pots containing potential host plants. Potted seedlings and potential hosts then were transplanted to field sites adjacent to a population of *S. americana* from which the seed had been collected. Germination of seedlings was >90% after a wet-cold treatment; a dry-cold treatment resulted in low germination. Seedlings grown in association with seedlings of the grass *Schizachyrium scoparium* did not differ in size or longevity from seedlings grown alone. Growth of seedlings was slightly greater in the presence of host plants than without, but seedlings still achieved only limited size in greenhouse conditions before transplantation (2 to 4 mm in width and height). After transplantation to the field the majority of seedlings died rapidly, but several persisted for over 45 days without showing appreciable growth. Poor seedling establishment and survival are believed to contribute to the rarity of this species. The development of improved methods for the propagation and transplantation of *S. americana,* and the greater understanding of the causes for the rarity of this endangered species, will increase options for recovery strategies.

Key Words: *Schwalbea americana,* hemiparasite, Scrophulariaceae, endangered species, propagation, species reintroduction, New Jersey

Schwalbea americana L. is a hemiparasitic, herbaceous perennial which was Federally listed as endangered in 1992 (U.S. Fish and Wildlife Service 1992). *Schwalbea americana* is a showy flowering plant with purplish yellow, bee pollinated, tubular flowers on an unbranched, pubescent, spike-like raceme (Sandhills Field Office 1993; Gleason and Cronquist 1991). As a hemiparasite, it attaches to the roots of a host plant through haustoria which allow the extraction of water, organic substances, and inorganic nutrients (Matthies 1995).

Schwalbea americana is thought to be one of the few species of an ancient Miocene flora to have survived the Pleistocene glaciation (Pennell 1935). It is monotypic, the most primitive member of the tribe Euphrasieae in the Scrophulariaceae, and always has been considered rare (Pennell 1935). Pennell (1935) originally separated the northern and southern populations of *Schwalbea* into two species, *S. americana* in the north and *S. australis* Pennell in the south. Fernald (1937) found instead that morphological variation between the two species had wide overlap and therefore they were combined into one species.

Habitat loss through development and fire suppression is thought to be responsible for the decline of this species (U.S. Fish and Wildlife Service 1994). The one population remaining in New Jersey, out of 18 historical occurrences, represents the current northernmost limit of the species' range. The species once extended into southern New England, but has not been found even where suitable habitat persists (Sorrie 1987). Other surviving locations are on the southeastern Coastal Plain, where the species occurs in longleaf pine (*Pinus palustris* Miller) savannas, flatwoods, and ecotonal areas between pine uplands and wetland depressions (Sandhills Field Office 1993; U.S. Fish and Wildlife Service 1992). It occurs in sandy, acidic soils and high light where frequent fire is often a factor in maintaining an open canopy and sparse vegetation (U.S. Fish and Wildlife Service 1992). Decreased fire frequency and suppression of the natural fire regime is considered a factor which has reduced the amount of available habitat for the species and resulted in the extirpation of some known populations of *Schwalbea americana* (U.S. Fish and Wildlife Service 1992).

The habitat requirements for this species include a fluctuating water table and open, early successional pine lowland habitat (U.S. Fish and Wildlife Service 1992). For a species to persist, it must either have the ability to track the shifting mosaic of available habitat through dispersal and re-establishment, or good conditions must be maintained locally (Thomas 1994). For *Schwalbea americana,* the persistence of locally favorable conditions would require the long-term maintenance of early successional habitat. As locations of *S. americana* are eliminated due to succession or anthropogenic habitat destruction and fire suppression, the species has not been observed in locally good habitat near historical locations (U.S. Fish and Wildlife Service 1992). The anthropogenic impacts on *S. americana* correspond with the predictions of Fiedler and Ahouse (1992), who indicated that long persisting but narrowly distributed species would be especially susceptible to human impact. *Schwalbea americana* would be considered to be in this category due to its Miocene origin (Pennell 1935) and rigid ecotonal habitat requirements.

There are many common hemiparasitic species, so the hemiparasitic nature of the species' biology is not necessarily a factor contributing to the rarity of *Schwalbea americana.* Hemiparasites are believed to have low resource-use efficiency and are often restricted to nutrient-poor habitats (Matthies 1995). The propagation of hemiparasitic plants generally is considered difficult, and past attempts to grow *S. americana* in the absence of host plants have resulted in the eventual death of all seedlings (Brumback 1989). Musselman and Mann (1977) grew seedlings of *S. americana* in association with several host species and concluded that it was a non-host-specific, obligate root parasite. In this study, the propagation of the species was initiated in order to provide plants for reintroduction to and expansion of the New Jersey population. A seed collection strategy was devised to maximize the sampling of genetic variability in the population, while minimizing the amount of seed taken from the population (Obee 1993).

MATERIALS AND METHODS

Seed germination and growth trials alone and with *Schizachyrium scoparium.* Seeds were collected on August 23, 1993, from 12 genets of *Schwalbea americana* at the one remaining population in New Jersey. Seeds were collected from no more than one capsule per ramet and no more than two capsules per genet. Genets producing less than five flowers were excluded from collection. Seeds were stored at room temperature after collection and a wet-cold treatment was initiated after approximately 3.5 mo. For the wet-cold treatment, seeds were placed on moist, absorbent germination paper in plastic sandwich boxes in a cold room at Nelson Hall, Rutgers University, and maintained in the dark at a temperature of 4°C. Light levels and temperature in this cold treatment fluctuated on occasion due to several temporary power losses and the sporadic turning on of lights in the room.

Germination commenced after approximately 4 mo., after which seedlings were transplanted into 25 cm^2 black plastic flats with various soil mixtures. Using tweezers, seedlings were placed into small soil depressions and gently covered with grains of sand. Different combinations of a coarse builder's sand, New Jersey Piedmont loam topsoil, vermiculite, Pro Mix BX (Premiere Brands, Inc., Stamford, CT), or a standard soil mix were used to create soil mixtures varying in texture and drainage capacity. The standard soil mix consisted of, by volume, 12 parts New Jersey Piedmont loam soil, 8 parts sand, 6 parts Canadian sphagnum peat, and 0.125 parts lime. The five additional soil combination ratios used were: (1) 2 sand : 1 vermiculite : 1 standard soil mix; (2) 1 sand : 1 Pro Mix BX: 1 topsoil; (3) 1 sand : 1 vermiculite; (4) 1 sand : 1 standard soil mix; (5) 2 sand : 1 Pro Mix BX: 1 topsoil.

Each of the soil mixtures had three replicate flats planted with *Schwalbea americana* in concentrations from 45 to 120 seedlings from up to six genotypes. Two flats of each soil combination (only 1 for soil mixture #4) also were sowed with approximately 100 seeds of a southern New Jersey population of *Schizachyrium scoparium* (Michx.) Nash (little bluestem) to serve as a potential host species for the *Schwalbea* seedlings. One of the flats of soil mixture #4 without *Schizachyrium* varied in transplantation technique. Strips of germination paper containing approximately 175 germinated seedlings of *Schwalbea* were placed upon the soil surface instead of having individual seedlings transplanted into soil depressions. Flats were maintained in a greenhouse low-light mist room, which kept the soil surface constantly moist.

Several trials were made in pots containing adult plants of *Schizachyrium scoparium* rather than seedlings. Each of two adult plants of *Schizachyrium* were planted with 15 seedlings of *Schwalbea americana* growing in 15 cm clay pots in the standard soil mix. Several hundred seeds of *Schwalbea* were added to the upper 1 cm of soil surface with two additional adult *Schizachyrium* plants. The *Schizachyrium* had been overwintered outside in 15 cm clay pots inserted in soil to the rim of the pots.

Seed germination and growth trials with Pine Barrens species. Pots containing potential host plants of New Jersey Pine

Barrens species were established on July 28, 1994. Host plants from the roadside and along a path near the present *Schwalbea americana* population were located. Roots were severed in a 15 cm diameter around the stem and transplanted with surrounding soil into 15 cm round black plastic pots. These plants, initially containing only limited root systems, were fertilized with NPK 20-20-20 and maintained in the greenhouse. Several Pine Barrens species were collected, some of which were identified as suitable host species for *S. americana* by Musselman and Mann (1977). The species were collected and labeled as follows: *Pinus rigida* Miller (pitch pine; Pot #1), *Vaccinium corymbosum* L. (high bush blueberry; Pots #2 and 4), *Gaultheria procumbens* L. (teaberry; Pot #3), *Ilex glabra* (L.) A. Gray (inkberry; Pots #5 and 6), *Quercus marilandica* Muenchh. (blackjack oak; Pot #7), *Prunus serotina* Ehrh. (black cherry; Pot #8), and *Gaylussacia dumosa* (Andr.) T. & G. (black huckleberry; Pot #9).

Seeds of *Schwalbea americana* were collected again on October 2, 1994, and the seeds were placed on germination paper under the same conditions as the previous year. Seeds were stored under one of two conditions: wet-cold using the same methods as described previously, or dry-cold. Wet-cold germinated seedlings were maintained moist at room temperature in indirect light for 7 days and then transplanted into the nine pots containing host plants maintained in the greenhouse. Pots containing host plants and wet-cold seedling transplants were maintained initially in the greenhouse mist room in approximately 15% of full sunlight. Then, 14–21 days later, 7 of the 9 pots were moved into 80% of full sunlight where they were bottom-watered from trays beneath the pots. After 1 mo., pots were moved back into the mist room to minimize chances of desiccation of seedlings.

Several germination trials were completed with seeds stored dry-cold. After approximately 5 mo., water was added to 30 seeds, half of which were placed in the laboratory at room temperature and half placed back into the previous cold treatment. After approximately 7 mo. of dry-cold storage, 80 seeds were placed in a germinator at a temperature of 30°C (day)/20°C (night) for 14 days and then switched to 20°C (day)/10°C (night) for 14 days.

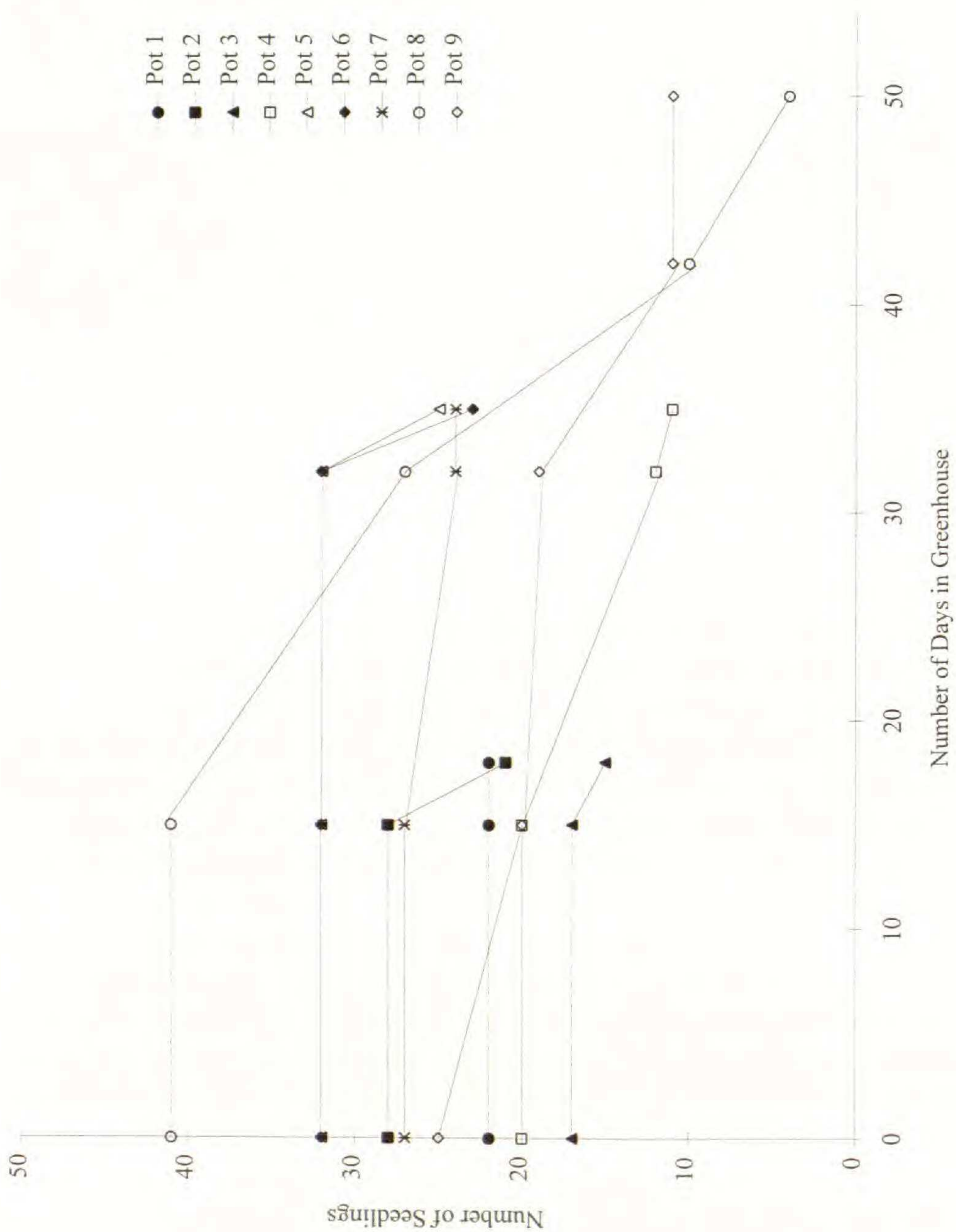
Reintroduction of seedlings. Seedlings were transplanted adjacent to the present population on three occasions. On April

21, 1995, seedlings with hosts in Pots 1–3 were transplanted to locations of similar habitat adjacent to the New Jersey population. These transplants were watered with 2 liters of water each, 1–2 times a week as needed, for 3–4 weeks after transplantation. Pots were cut away from soil clumps which were placed whole, without disturbing seedlings, into carefully cut holes in the ground and watered directly. Two of the transplants had two layers of white cheesecloth placed on wood stakes 1 ft. above the transplants, each covering an area of 1 m^2. The third transplant had no cheesecloth but was placed in a shady area near the forest edge. Cheesecloth was removed from the transplants after one week. On May 8, Pots 4–7 were transplanted adjacent to the existing natural population. These plants were shaded with cheesecloth; remaining seedlings from the previous transplant were shaded again with cheesecloth. On May 23, the remaining greenhouse seedlings in Pots 8 and 9 were transplanted adjacent to the existing population and shaded with cheesecloth.

RESULTS

Seedlings with and without *Schizachyrium scoparium*. Seeds were observed to have germinated in the wet-cold treatment on April 6, 1994, approximately 4 mo. after the initiation of the treatment. Seeds from 10 of the 12 genets germinated at >90%. Seeds from the remaining 2 genets did not germinate due to fungal contamination during the cold treatment. Germinated seedlings were yellowish-green in color with rigid radicles 1–3 mm in length.

Seedlings persisted after transplantation to flats for up to 2 mo. with slow mortality. No differences in vigor or survival were observed between soil treatments, with or without potential host plant *Schizachyrium scoparium,* or based upon genet. Seedlings growing on germination paper placed on the soil surface persisted for 2–5 weeks but failed to develop an extended root system. Seedlings generally did not grow any larger than when planted, i.e., only 2–4 mm in width and height with a single set of cotyledons. However, approximately 10% of seedlings exhibited slight growth and developed a second set of leaves. Seedlings planted with adult *Schizachyrium* did not differ in vigor or survival from other treatments without hosts or with seedling *Schizachyrium*, and died within 2 mo. No germination of *Schwalbea*


Pot 1
Pot 2
Pot 3
Pot 4
Pot 5
Pot 6
Pot 7
Pot 8
Pot 9
Number of Seedlings
0
10
20
30
40
50
Number of Days in Greenhouse
0
10
20
30
40
50

americana was observed from seed overwintered with adult *Schizachyrium.*

Seedlings with Pine Barrens plants. The wet-cold treated seedlings of *Schwalbea americana* were observed to have germinated on February 21, 1995, and transplantation after 7 days resulted in 200–300 established seedlings. By March 23, several plants were observed developing a set of leaves past the initial cotyledons. Seedlings persisted in the pots at a steady state, with negligible growth or mortality. Numbers of seedlings in each pot were recorded beginning April 3 (Figure 1). The rate of mortality remained low over the next 2.5 weeks. As the rate of mortality started to increase, transplantation from pots to the field was initiated. No differences in seedling mortality or growth based upon host plants in the pots were apparent (Figure 1). A firm association could not be made between host species and seedling survival due to insufficient replication and high mortality of seedlings.

No germination was observed from seeds stored dry-cold after the addition of water at room temperature or in a 4°C cold treatment. Of seeds stored dry-cold and incubated in fluctuating temperatures, only 2 of 80 seeds germinated 1 mo. later.

Reintroduction of seedlings. The number of seedlings remaining in each transplant to the field decreased to 0 in most cases from 18–45 days after time of transplantation (Figure 2). By 70 days only 5 seedlings remained viable. No specific host plant produced longer persistence of seedlings or greater growth (Figure 2). Most seedlings from the first reintroduction (Pots 1–3) died within 18 days but some in Pot 2 persisted as long as the

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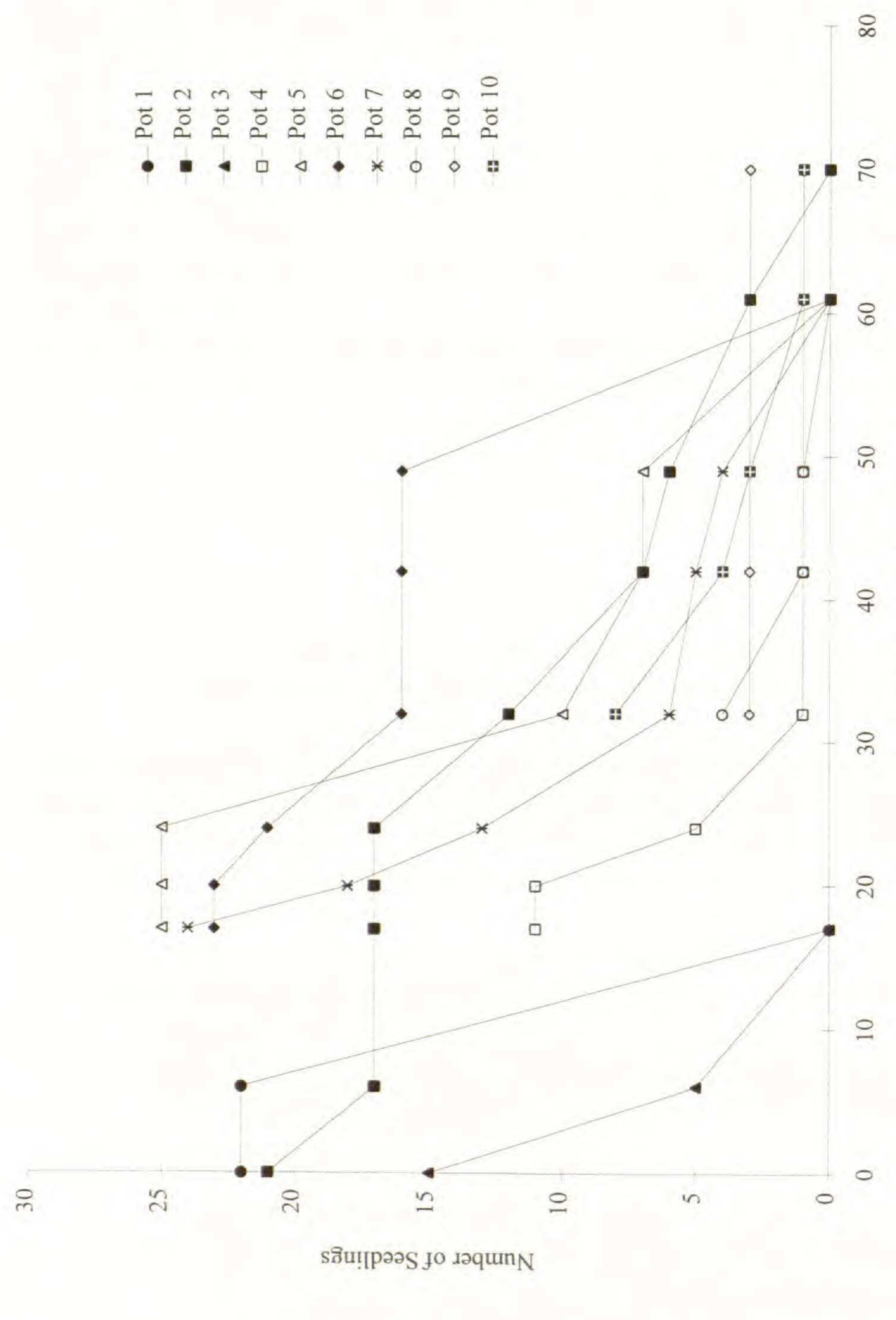
Figure 1. Number of seedlings over time in each of nine pots located in a greenhouse. The last data point for each pot indicates the time at which seedlings were transplanted to field conditions. Day 0 indicates the time at which the collection of mortality data was initiated, on April 3. Species in each pot were as follows: *Pinus rigida* (pitch pine; Pot #1), *Vaccinium corymbosum* (high bush blueberry; Pots #2, 4), *Gaultheria procumbens* (teaberry; Pot #3), *Ilex glabra* (inkberry; Pots #5, 6), *Quercus marilandica* (blackjack oak; Pot #7), *Prunus serotina* (black cherry; Pot #8), and *Gaylussacia dumosa* (black huckleberry; Pot #9).


Pot 1
Pot 2
Pot 3
Pot 4
Pot 5
Pot 6
Pot 7
Pot 8
Pot 9
Pot 10
Number of Seedlings
0
5
10
15
20
25
30
Number of Days in Field
0
10
20
30
40
50
60
70
80

seedlings from the second reintroduction (Figure 2). Time of reintroduction affected the initial size of seedlings, with later reintroductions composed of larger seedlings. Only the third reintroduction (Pots 8–10) produced seedlings which persisted until the end of the growing season (Figure 2). Most of these seedlings were initially larger in size when transplanted than previous seedlings, and included four seedlings with leaf spans of 1.2–1.7 cm and heights of 1.0–1.4 cm. Other seedlings were usually less than 1 cm in height and width at time of reintroduction.

DISCUSSION

The greater germination of cold-stratified seeds found for *Schwalbea americana* is common among temperate species and has been found for other hemiparasitic species (Baskin et al. 1991; Masselink 1980). The low germination of dry-cold treated seed is presumed to be due to lack of sufficient conditions to break physiological dormancy. Dormant seeds would have the ability to form a long-term seed bank for *S. americana.* However, the firm but small and fragile seeds are easily damaged, which may limit long-term seed banking ability. The small seed size of many obligate root parasites has been suggested by Musselman and Mann (1977) to be an adaptation for filtering through vegetation and litter to germinate as close as possible to a host plant. Seeds in this study were germinated in the absence of root exudates from potential host plants. Root exudates have been found necessary for germination of some hemiparasites such as *Striga* spp. and *Orobanche minor* J.E. Smith (Sunderland 1960; Vallance 1950). Numerous other hemiparasites, however, are able to germinate without chemical interactions with host roots (Baskin et

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Figure 2. Number of seedlings over time in ten seedling and host plant transplants to field conditions. Transplants occurred at three time points, Days 0, 17, and 32. Pot transplants 9 and 10 each originate from greenhouse Pot 9, which was divided into two sections at the time of transplant. Species in each greenhouse pot were as follows: *Pinus rigida* (pitch pine; Pot #1), *Vaccinium corymbosum* (high bush blueberry; Pots #2, 4), *Gaultheria procumbens* (teaberry; Pot #3), *Ilex glabra* (inkberry; Pots #5, 6), *Quercus marilandica* (blackjack oak; Pot #7), *Prunus serotina* (black cherry; Pot #8), and *Gaylussacia dumosa* (black huckleberry; Pot #9).

al. 1991; King 1989; Masselink 1980; Sahai and Shivanna 1985; Vallance 1951, 1952).

The effect of hemiparasitism on seedling establishment of *Schwalbea americana* is not known. The presence of haustorial connections between *S. americana* seedlings and potential host plants was not investigated due to the limited number of seedlings and host plants. The seedlings of *S. americana* in this study may or may not have established haustorial connections with host plants. Differences in survival or growth of seedlings could not be attributed to specific host plants (Figures 1 and 2). The presence of young seedlings of *Schizachyrium scoparium* also was not successful in stimulating growth of *Schwalbea.* Seedlings growing with woody Pine Barrens species achieved slightly greater size than those growing with *Schizachyrium.* However, this may be due to the use of natural soil instead of artificial soil mixtures rather than to differences among the host species. The general lack of growth of seedlings of *Schwalbea* implies that haustorial connections may be necessary at an early developmental stage. For some other hemiparasitic species, fertilization has been known to replace the necessity for a host species (Lackney 1981; Mann and Musselman 1981). Connections to host plants were observed in the successful cultivation of another rare hemiparasite, the annual *Agalinis auriculata* (Michx.) S. F. Blake [as *Tomanthera auriculata* (Michx.) Raf.], which was grown with host plants in greenhouse studies (Cunningham and Parr 1990). However, preliminary efforts to grow *T. auriculata* resulted in small seedlings which eventually withered and died, similar to many seedlings of *Schwalbea* in this study (Cunningham and Parr 1990).

Seedling establishment of *Schwalbea americana* is believed to take place in early spring when late frosts may have a negative effect on survival. The ability of seeds to germinate at low temperatures in this study indicates that early seedlings may be produced, which then would be susceptible to temperature related mortality. Transplanted seedlings were observed to turn a reddish color after being put into the field and exposed to temperatures ranging down to 5°C. Leaves of adult *S. americana* plants are purple tinged early in the spring and turn greener as the season progresses and temperatures rise.

The increased greenhouse cultivation period required to produce larger seedlings resulted in greater growth but high mortality

(Figure 1). However, these larger seedlings were more successful in becoming established in the field and long-term survival is more likely for these seedlings (Figure 2). The success of future transplants will be dependent upon the development of improved greenhouse techniques. The primary difficulty in growing plants in the greenhouse to a size which would be likely to survive transplantation to the field may lie in re-creating fluctuating moisture conditions common in ecotonal areas. The seedlings in this study were maintained in continuously moist rather than fluctuating conditions, and were maintained in low light to prevent desiccation. Continued experimentation with artificial growing conditions for *Schwalbea americana* seedlings should concentrate upon growing larger plants in a greenhouse or a growth chamber, in higher light, in natural soils with fluctuating moisture levels, and in the presence of host plants.

The results of this study support the hypothesis that poor seedling establishment and survival contribute to the rarity of this species. After very high germination of seed, survival was poor both in artificial greenhouse conditions and after transplantation to suitable habitat (Figures 1 and 2). This corresponds with the lack of observation of seedlings in the field and the poor colonization of new habitat by *Schwalbea americana.* As habitat destruction continues through fire suppression, succession, or outright destruction, this species is likely to continue to decline (U.S. Fish and Wildlife Service 1992). The development of improved methods for the propagation and transplantation of *S. americana* may be critical to the persistence of the species, and will increase options for recovery through population expansion and reintroduction.

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